ing that exceeds the likely precipitation and sea ice changes and carries a low $\delta^{18}O$ signal also suggests an acceleration in the melting rate of West Antarctic ice shelves east of the Ross Sea.

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The Function of the Cranial Crest and Jaws of a Unique Pterosaur from the Early Cretaceous of Brazil

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The discovery of a previously undescribed pterosaur, *Thalassodromeus sethi*, yields information on the function of cranial crests and the feeding strategy developed by these extinct flying reptiles. The material consists of a large skull (length: 1420 millimeters, including the crest) with a huge bony crest that was well irrigated by blood vessels and may have been used for regulation of its body temperature. The rostrum consists of two bladelike laminae, the arrangement of which is analogous to the condition found in the bird *Rynchops*, which skims over the water to catch food, indicating that *T. sethi* also may have been a skimmer.

Despite being studied for over 200 years, the overall knowledge of pterosaur diversity and biology is rather slim, mainly due to uneven sampling and the generally poor preservation of specimens (*1*, *2*). Moreover, because pterosaurs are extinct, their biological habits and functions of anatomical features are difficult to establish, and most interpretations have relied on comparisons with modern analogs such as birds. Here, we report a previously undescribed pterosaur that shows a distinct morphology of the skull, providing information on the function of cranial crests and feeding strategy. The specimen comes from the Romualdo Member of the Santana Formation (*3*), in the Araripe Basin, in northeastern Brazil, which is one of the few deposits where pterosaurs are found in large numbers with good preservation.

The sedimentary rocks of the Santana Formation were deposited during the Early Cretaceous (Aptian/Albian) and represent two distinct *lagerstatten*, formed by the lacustrine limestone layers of the Crato Member at the base and the lagoonal limestone concretions embedded in shales of the Romualdo Member at the top (*4*, *5*). Although pterosaurs have been found in the lower layers (*2*, *6*–*8*), the deposits in the Romualdo Member contain better-preserved specimens (*9*–*12*). The material described here was preserved in a calcareous nodule from this deposit and consists of an almost complete skull (Fig. 1), representing a new species.

Pterosauria Kaup, 1834
Pterodactyloidea Plieninger, 1901
Tapejaridae Kellner, 1989
Thalassodromeus nov. gen.
T. sethi nov. sp.

Etymology: *Thalassodromeus* from the Greek thálassa (= sea) + dromeús (runner) meaning the "sea runner"; *sethi* for the ancient Egyptian god Seth.

Holotype: skull (total length, 1420 mm; length from the squamosal to the tip of the premaxilla, 798 mm) and lower jaw (length: preserved, 635 mm; estimated, 710 mm) deposited at the Museu de Ciências da Terra/Departamento Nacional de Produção Mineral (DGM 1476-R) (Figs. 1 to 3); cast at the Museu Nacional (MN)/Universidade Federal do Rio de Janeiro (UFRJ) (MN 6678-V).

Horizon and locality: The specimen was collected in 1983 at the outcrops of the Romualdo Member [Albian (*3*, *5*)], in the Santana Formation, near the town of Santana do Cariri, in the state of Ceará, northeastern Brazil.

Diagnosis: Tapejarid with developed cranial crest composed of premaxillae, frontal, parietal, and supraoccipital, starting at the tip of the skull and extended posteriorly, well behind the occipital region; posterior end of the cranial crest V-shaped; suture between premaxillae and frontoparietal portion of the crest rectilinear; anterior portion of the premaxillae and dentary with sharp dorsal and ventral edges; palatines before palatal crest strongly concave; posterior (occipital) region broader than in other tapejarids (width over quadrates, 20% of squamosal to premaxilla length).

With the exception of two segments from the ventral part of the skull plus the mandible and the distal tip of the lower jaw, the material is complete and all bones are preserved in three dimensions. The only signs of compaction are found in the region of the left jugal and in the right mandibular ramus, which are slightly pushed inward.

As is typical of derived pterosaurs (members of the clade Pterodactyloidea), *T. sethi* has an elongated skull (Fig. 1). The orbit is positioned lower than the dorsal rim of the antorbital fenestra, a feature only present in the azhdarchids [e.g., *Quetzalcoatlus* sp.

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(*13*)] and tapejarids [*Tapejara wellnhoferi* (*14*, *15*)]. The nasoantorbital fenestra is very large (390 mm), comprising about half of the cranial length between the squamosal and the tip of the premaxilla. Starting at the anterior end of the premaxillae, *T. sethi* exhibits a large sagittal crest that extends above the nasoantorbital fenestra and well behind the occipital region. This cranial structure is formed by frontals, parietals, and premaxillae, which fuse in the midline, and by the supraoccipital, which builds the ventral edge right behind the occipital region. Despite its size, the crest is lightly built, with the bones united by a well-developed trabecular system. The premaxillae contribute to most of it and differ from those of other crested pterosaurs [e.g., *Pteranodon* (*16*, *17*) and *Dsungaripterus* (*18*)], because they extend to the most posterior portion of the crest, terminating in a V-shaped structure. The frontals and parietals form the base of the posterior part of the crest, and their contact with the premaxillae is straight. This crest is essentially hollow, internally supported by a well-developed system of trabeculae, and varies in thickness (from 1.0 to 10.5 mm) along the region where it connects to the skull. Above the skull roof, it thickens at the contact between the premaxilla and frontal and gets gradually thinner toward the top and back, except for the ventral part directly behind the occiput (formed by the supraoccipital), where it has a thick base (7.5 mm) and shows several ridges for muscle attachment.

On the basis of the large sagittal crest and the extended nasoantorbital fenestra, *T. sethi* can be allocated to the Tapejaridae (*19*). Two other genera, *Tapejara* (*7*, *14*) and *Tupuxuara* (*20*, *21*), each with two species, have been grouped in this clade. *Thalassodromeus* is easily set apart from *Tapejara*, which are comparatively short-faced pterosaurs. *Thalassodromeus* shares with *Tupuxuara* a palatal crest but has the anterior portion of the palatal region turned into a bladelike lamina instead of the flat condition found in *Tupuxuara*. Furthermore, the palate posterior to the palatal crest of the new taxon is concave instead of having the convex condition found in *Tupuxuara* (*20*). *Thalassodromeus* also has a proportionally higher premaxillary sagittal crest, particularly above the nasoantorbital fenestra. A briefly mentioned skull of *Tupuxuara* (*22*) shows that the occipital region of *Thalassodromeus* is comparatively broader. Some fragmentary pterosaur remains from Maastrichtian strata of Romania include a large occiput (*23*), but the material lacks the anterior portion of the skull, impeding detailed comparisons with *Thalassodromeus*.

With the exception of *Tapejara imperator* (*7*), *T. sethi* has the proportionally largest crest known in any vertebrate (fossil or recent), which makes up about 75% of the

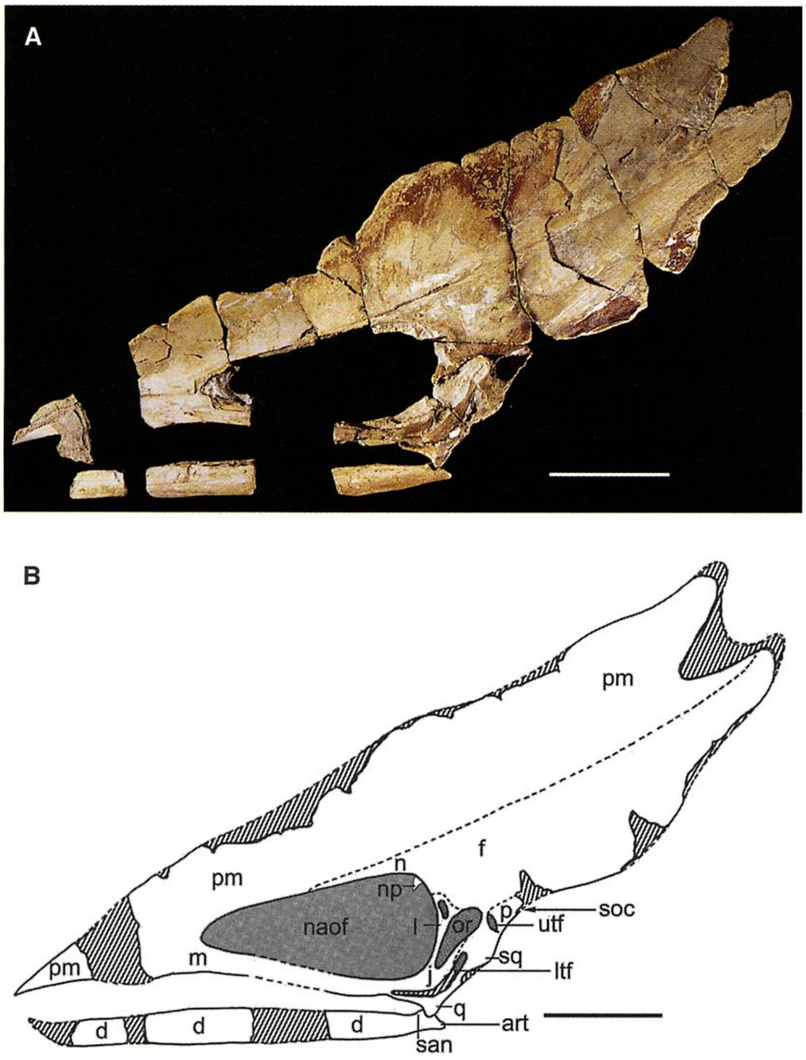

Fig. 1. (**A**) *T. sethi* (DGM 1476-R) skull in left lateral view. (**B**) Drawing showing the contact of the cranial bones. Art, articular; f, frontal; d, dentary; j, jugal; l, lacrimal; ltf, lower temporal fenestra; m, maxilla; naof, nasoantorbital fenestra; n, nasal; np, nasal process; or, orbit; p, parietal; pm, premaxilla; q, quadrate; san, surangular; soc, supraoccipital; sq, squamosal; utf, upper temporal fenestra. Scale bar, 200 mm.

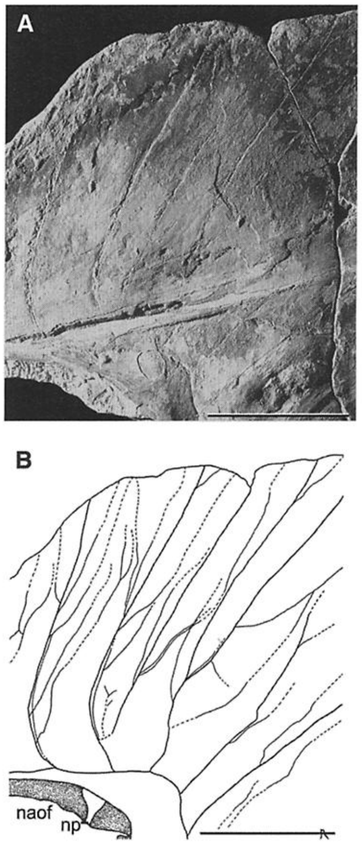

Fig. 2. (**A**) Detail of the crest of *T. sethi* (DGM 1476-R), showing channels on the bone surface, interpreted as the imprints of blood vessels. (**B**) Drawing showing the preferential orientation of the interpreted blood vessels (only the larger ones are illustrated here). The stippled area indicates sedimentary rock. Naof, nasoantorbital fenestra; np, nasal process. Scale bar, 100 mm.

cranial lateral surface. The crest in *T. sethi* differs from the one in *T. imperator*, because it is fully ossified, with some darker areas suggesting that it had a horny covering, particularly on the top and posterior end. A system of channels of different sizes and thicknesses is present on the external bone surface (Fig. 2A). This feature, observed for the first time in a pterosaur cranial crest, is interpreted as the impression of blood vessels. A main central channel rises vertically from above the orbit and is divided into large channels directed anteroposteriorly at the basal portion of the crest. From those, other channels branch off, curve upward, and tend to be parallel to each other, giving rise to smaller ones that form a complex pattern (Fig. 2, A and B). This network of vascular supply indicates that this crest was extensively irrigated by blood vessels and is consistent with the notion of it having been used in thermoregulation, as has been argued for some dinosaurs (*24*, *25*). In *Thalassodromeus*, this cranial structure might have been more useful for cooling, with the crest used as a heat dissipater enabling the animal to lose excess metabolic heat to the environment through convection. The large size of the crest increased the surface area for that purpose, but the heat transfer effectiveness must have been controlled by, and been dependent on, the ability of the circulatory system to pump blood to the crest, for which a well-developed network of vascular supply was necessary. To be able to control the body temperature might have been particularly useful when the animal was most active, as, for example, during hunting, when it would dump excess metabolic heat into the environment, with the crest having a wind-aligned orientation, with effectiveness being eventually increased by restricted intentional lateral movement of the head.

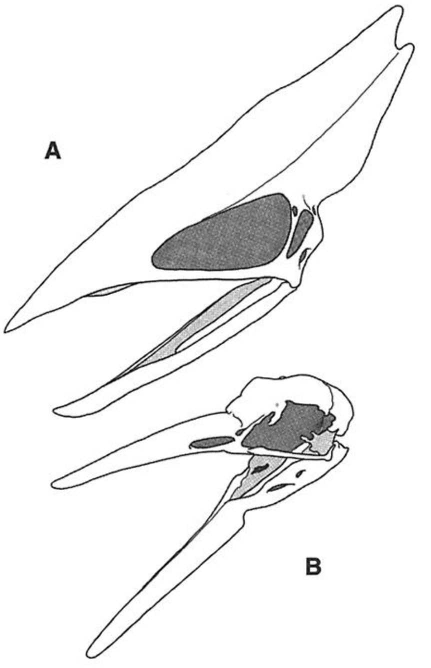

Fig. 3. The skull of *T. sethi* (**A**) and *Rynchops* (**B**). Note the extreme lateral-compressed and scissors-like upper and lower jaws of both (not drawn to scale).

It should be noted that a thermoregulatory function of the crest would not preclude this structure from having had other functions, such as species recognition, with the particular form (including the V-shaped end), in conjunction with colors, allowing members of *T. sethi* to recognize their kin. Sexual dimorphism is also a possibility and has been argued for *Pteranodon* [all having cranial crests (*26*, *27*)], but the limited information on tapejarid postcranials makes this last hypothesis complicated to test. Although the function of cranial crests in pterosaurs is difficult to determine (*14*, *17*, *18*, *26*–*29*), all evidence suggests that, in *T. sethi*, this structure had multiple functions, interfering with aerodynamics (because of its large size), helping in thermal regulation, and functioning as a display structure.

The palatal and rostral configuration of *T. sethi* is also unusual and is related to its feeding habit. A strong concavity formed by the palatines and bordered laterally by the maxillae is present under the anterior half of the nasoantorbital fenestrae. Anterior to this concavity, the palate is convex, forming a short ventral keel that turns into a sharp blade anteriorly. The fused dentaries form a perfect counterpart to the palate, with a developed concavity, followed by a short, deep groove (that during occlusion encases the palatal keel, forming a strong interlocking mechanism) and an anterior sharp bony blade (Fig. 3A). Between both blades there is a gap. The whole skull, particularly the rostral portion, is streamlined.

The only modern analog with such a rostral end is found in the avian genus *Rynchops* (Laridae; Rynchopini). Popularly known as skimmers, the members of this taxon have laterally compressed upper and lower jaws with a blade-like horny covering (rhamphotheca) and a protruding lower jaw, giving it, in lateral view, an asymmetric scissors-like aspect (Fig. 3B). *Rynchops*, whose wing span is generally less than 1 meter, skims over the surface and dips its lower jaw into the water to catch small pelagic fishes and crustaceans (*30*). In addition to the rostrum, these birds have other structural adaptations for skimming, among which are curved tomia (the cutting edge of the rhamphotheca) of the upper jaw, broad quadrate condyles, large palatines, large neck musculature, large adductor mandibula complex musculature, and greater blood supply and enervation of the tips of the jaws, particularly the lower one (*30*).

The palatines of *T. sethi* are enlarged too, but unlike those of *Rynchops* and other pterosaurs, they are concave, constituting a possible adaptation for momentarily storing food. The occipital region of *T. sethi* is more developed (width between opisthotics = 113.6 mm) than in other pterosaurs, with strong muscle scars in several parts and a well-developed supraoccipital crest, suggesting the presence of powerful neck muscles. Several ridges that reach the base of the basal portion of the sagittal crest behind the occipital region are observed above the temporal opening, indicating that the adductor musculature was well developed. Lastly, there are several small foramina on the tip of the premaxillae (the tip of the dentary is not preserved) indicating that this region was well irrigated by blood vessels (and likely well supplied by nerves). The morphology of the specimen supports the hypothesis that *T. sethi* was also a skimmer. As in *Rynchops*, the specialized scissors-like bill of *Thalassodromeus* almost precludes any other method of capturing prey, such as swooping toward the water and taking the prey with a single downward nod of the head, as observed in several birds [e.g., gull-billed tern (*30*)]. Because of the large but thin crest, it is also unlikely that *Thalassodromeus* plunged in the water for fish, as observed, for example, in the royal tern (*30*).

Although the fishing technique of *T. sethi* is difficult to reconstruct, we have used detailed reports of the skimming technique of *Rynchops* (*30*) to develop a model, which also takes into account the differences between the basic avian and pterosaurian skeletons (figs. S1 and S2). Whenever striking an object during skimming, the upper jaw of *Rynchops* clamps down, while the head moves down and back, sometimes becoming completely submerged. The pterosaur neck is formed usually by nine cervicals (*1*, *12*, *17*) [compared to the 15 cervicals of *Rynchops* (*30*)], limiting its mobility, as compared to *Rynchops*. Therefore, although the general downward movement of the head of *Thalassodromeus* was similar to that of *Rynchops*, the backward motion was more limited. Furthermore, the size of the crest would impede a complete submersion of the skull, contrary to what occasionally happens in *Rynchops*. During skimming, this bird maintains its body in a horizontal or only slightly tilted position relative to the water surface, alternately gliding or flapping rapidly with regular beats (*30*). Based on its large wing surface, *Thalassodromeus* probably used more gliding power during skimming, occasionally flapping its wings, particularly after catching prey.

The rostral configuration of *T. sethi* is unique among pterosaurs. The most similar condition is found in some species of *Rhamphorhynchus* from the Late Jurassic Solnhofen limestone (*31*), which have a small anterior projection on the tip of the lower jaw and have been regarded as "casual skimmers"

(*1*). The rostral portion of the *Rhamphorhynchus* species differs from that of *Thalassodromeus* because it is toothed, is comparatively reduced, and has a less sharp and smaller anterior rostral projection. Furthermore, the skull in *Rhamphorhynchus* lacks the adaptations for skimming activity discussed above and might have had only crude and limited skimming behavior. Another difference between both is size. Although most *Rhamphorhynchus* specimens have a wingspan ranging from 500 to 1200 mm [the largest one being 1750 mm (*31*)], the estimated length represented by the type material of *Thalassodromeus sethi* [based on other tapejarid specimens (*8*, *22*)] varies between 4200 and 4500 mm, making it a large volant creature that got its nourishment by skimming the Araripe lagoon and the nearby ocean 110 million years ago.

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Supporting Online Material
www.sciencemag.org/cgi/content/full/297/5580/389/DC1
Figs. S1 and S2

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Generation and in Vitro Differentiation of a Spermatogonial Cell Line

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Spermatogenesis is the process by which spermatogonial stem cells divide and differentiate to produce sperm. In vitro sperm production has been difficult to achieve because of the lack of a culture system to maintain viable spermatogonia for long periods of time. Here we report the in vitro generation of spermatocytes and spermatids from telomerase-immortalized mouse type A spermatogonial cells in the presence of stem cell factor. This differentiation can occur in the absence of supportive cells. The immortalized spermatogonial cell line may serve as a powerful tool in elucidating the molecular mechanisms of spermatogenesis. Furthermore, through genomic modification and transplantation techniques, this male germ cell line may be used to generate transgenic mice and to develop germ cell gene therapy.

Spermatogonia originate from primordial germ cells (PGCs), which are derived from the epiblast by 7.5 days post coitum (dpc) and migrate through the dorsal mesentery and enter the developing fetal gonad, the genital ridge, between 10.5 and 12.5 dpc (*1*, *2*). Once

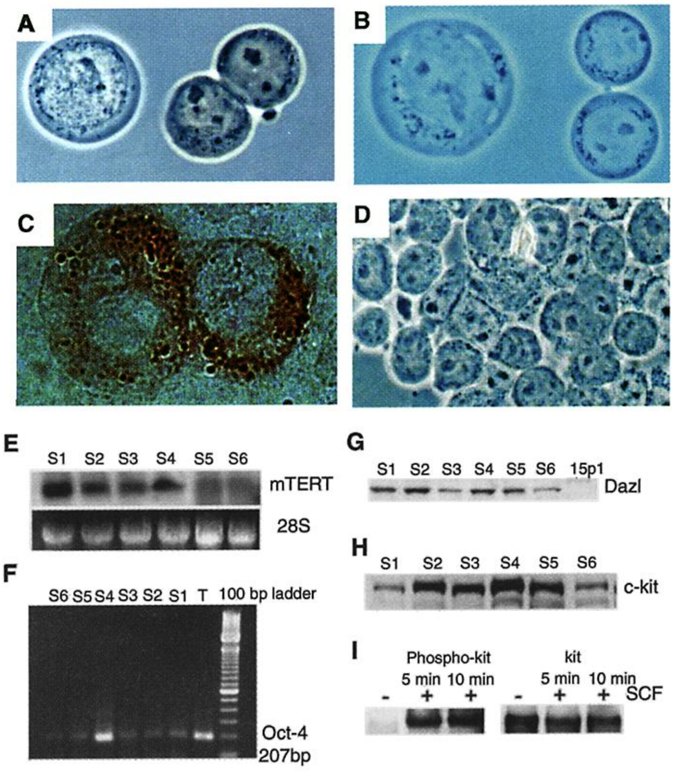

Fig. 1. Characterization of type A spermatogonial cell line. **(A)** After 2 months of culture, the immortalized cells displayed the typical morphology of type A spermatogonia, such as spherical nuclei and organelles in a perinuclear location. **(B)** Morphology of freshly isolated type A spermatogonia (control). **(C)** The immortalized cells were positive for c-kit, as shown by immunocytochemistry. **(D)** After subcloning and culture for 1 year, the immortalized cells still maintained the morphology of type A spermatogonia. **(E)** Northern blot (25 μg of total RNA for each lane) showing mTERT expression in cell lines S1 to S6. **(F)** Expression of Oct-4 in immortalized cells, shown by RT-PCR as a 207-bp product; lane T, control testis from newborn pups. **(G)** Dazl was expressed in all six cell clones, as shown by Western blot; the 15p-1 Sertoli cell line is a negative control. **(H)** c-kit was expressed in all six cell clones, as shown by Western blot. **(I)** After stimulation with mSCF (100 ng/ml) for 5 and 10 min, c-kit immunoprecipitates were probed for phosphotyrosine and reprobed for c-kit.